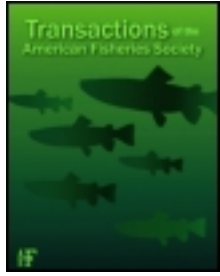


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Fall and Early Winter Movement and Habitat Use of Wild Brook Trout

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ARTICLE

Fall and Early Winter Movement and Habitat Use of Wild Brook Trout

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Abstract

Brook Trout *Salvelinus fontinalis* populations face a myriad of threats throughout the species' native range in the eastern United States. Understanding wild Brook Trout movement patterns and habitat requirements is essential for conserving existing populations and for restoring habitats that no longer support self-sustaining populations. To address uncertainties related to wild Brook Trout movements and habitat use, we radio-tracked 36 fish in a headwater stream system in central Pennsylvania during the fall and early winter of 2010–2011. We used generalized additive mixed models and discrete choice models with random effects to evaluate seasonal movement and habitat use, respectively. There was variability among fish in movement patterns; however, most of the movement was associated with the onset of the spawning season and was positively correlated with fish size and stream flow. There was heterogeneity among fish in selection of intermediate (0.26–0.44 m deep) and deep (0.44–1.06 m deep) residual pools, while all Brook Trout showed similar selection for shallow (0.10–0.26 m) residual pools. There was selection for shallow residual pools during the spawning season, followed by selection for deep residual pools as winter approached. Brook Trout demonstrated a threshold effect for habitat selection with respect to pool length, and selection for pools increased as average pool length increased up to approximately 30 m, and then use declined rapidly for pool habitats greater than 30 m in length. The heterogeneity and nonlinear dynamics of movement and habitat use of wild Brook Trout observed in this study underscores two important points: (1) linear models may not always provide an accurate description of movement and habitat use, which can have implications for management, and (2) maintaining stream connectivity and habitat heterogeneity is important when managing self-sustaining Brook Trout populations.

Brook Trout *Salvelinus fontinalis*, a coldwater fish species native to eastern North America, has a range that begins in northern Georgia and extends northward along the Ap-

palachian Mountains and across the Laurentian Great Lakes region through a large portion of Canada to the Arctic Circle (MacCrimmon et al. 1971). Brook Trout have ecological, social,

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and economic importance; however, due to habitat loss, populations are declining over much of their native range and many are isolated and restricted to headwater stream systems (EBTJV 2008; Hudy 2008). The introduction of nonnative salmonids, specifically Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss*, has placed additional pressure on Brook Trout and has resulted in an additional challenge of managing sympatric populations (EBTJV 2008). Brook Trout have variable life histories, and populations can be either potamodromous (Mucha and Mackereth 2008) or anadromous (Doucett et al. 1999). Inland stream Brook Trout are typically resident (i.e., nonmigratory) fish that are relatively short lived, with a life span of 3 to 4 years. These resident stream populations are particularly vulnerable to alterations of the landscape and subsequent impacts on stream connectivity and habitat quality. In fact, much of the species' native range overlays the Marcellus shale formation, a major sedimentary bedrock unit under the Allegheny Plateau Region of North America and reservoir of natural gas that is predicted to be increasingly exploited over the next several decades (Entrekin et al. 2011). This development will have potentially large effects on the landscape mosaic currently supporting wild Brook Trout populations.

Although considerable research efforts have been devoted to understanding Brook Trout ecology (e.g., Fausch and White 1981; Cunjak and Green 1983; Marschall and Crowder 1996), there is a lack of complete understanding of seasonal movement dynamics and habitat use. In particular, there is uncertainty on how movement and habitat use vary over space and time, and how much heterogeneity exists in movement and habitat use both among populations and among individuals within populations. Furthermore, much of the published research that has studied movement and habitat use was focused on nonnative Brook Trout in western United States streams (e.g., Chisholm et al. 1987; Riley et al. 1992; Lindstrom and Hubert 2004). Studies that have examined wild Brook Trout movement in the eastern United States (e.g., Baird and Krueger 2003; Roghair and Dolloff 2005), although useful to understanding Brook Trout ecology, were often limited to less than 2 months duration and provided only coarse information with respect to physical habitat. Many of the current threats to Brook Trout populations may affect both stream connectivity and the quality of instream habitat, leading to increased importance of studies that examine movement and habitat use. Incomplete information pertaining to the ecology and life history of a fish species can lead to erroneous conclusions about population dynamics, genetic isolation of populations, and success of fisheries management activities (Gowan et al. 1994; Riley and Fausch 1995). Increased understanding of movement dynamics and habitat selection will aid researchers in identifying conditions that facilitate a species' establishment, persistence, and dispersal (DeGrandchamp et al. 2008). Specifically, knowledge of movement tendencies of Brook Trout combined with fish-habitat relationships can be used to help (1) direct conservation efforts to areas with habitat conditions deemed necessary for sustaining Brook

Trout populations, (2) assist with restoration programs by providing targets for stream restoration efforts, and (3) predict the consequences of potential habitat changes and management actions (Scheuerell et al. 2006; Knudby et al. 2010).

A variety of factors potentially influence movement and habitat use of Brook Trout. Many of these are associated with prespawning, spawning, and postspawning requirements, and increased movement is often observed in late summer to early winter (Curry et al. 2002; Peterson and Fausch 2003). Spawning of Brook Trout typically occurs during the fall, and important habitat characteristics for redd-site selection include stream flow velocity and substrate type (Witzel and MacCrimmon 1983; Bernier-Bourgault and Magnan 2002). Also, Brook Trout have been consistently observed to select areas of groundwater upwelling to construct redds in field studies (Witzel and MacCrimmon 1983; Snucins et al. 1992; Curry and Noakes 1995), laboratory experiments (Webster and Eiriksdottir 1976), and study ponds (Carline 1980). Increased movement during the fall also corresponds to changing water temperatures, which decrease into the range of thermal preference for Brook Trout (between 11°C and 16°C; Coutant 1977). Other factors that may influence stream-dwelling fish movement and habitat use include fish size (Bunnell et al. 1998; Quinn and Kwak 2011) and stream flow (Gowan and Fausch 1996; Albanese et al. 2004). The overall goal of our study was to evaluate seasonal movement and habitat use of wild Brook Trout in central Pennsylvania from late summer through early winter, a time period of importance both ecologically and from a management perspective. Our specific objectives were to (1) determine the temporal dynamics of Brook Trout movement and identify drivers (correlates) of fish movement and (2) evaluate seasonal Brook Trout habitat selection based on available residual pool habitat.

METHODS

Data Collection

Study area.—This research was conducted in central Pennsylvania (Figure 1). The main stem of the system was Fishing Creek, a 69-km-long limestone stream located in southern Clinton County. Although Fishing Creek was dominated by Brown Trout (estimated biomass of 268 kg/ha), self-sustaining wild Brook Trout populations are present (estimated biomass of 2 kg/ha) in several of the tributaries (PFBC 2009). In addition to Fishing Creek, the study area included three headwater tributaries: Cherry Run, Bear Run, and the unnamed tributary 22515 (hereafter referred to as UNT; Figure 1). Unlike Fishing Creek, these tributaries lack a limestone influence in the geology of the underlying aquifer. Cherry Run is referenced as both upper Cherry Run (the upstream portion) and lower Cherry Run (the downstream portion). This division of Cherry Run was a reflection of where Brook Trout were sampled. As a result of access points, fish were captured in the lower 5 km and the upper 5 km of the stream. Fish were not sampled in the middle 2 km reach (see Figure 1), but there were no barriers preventing

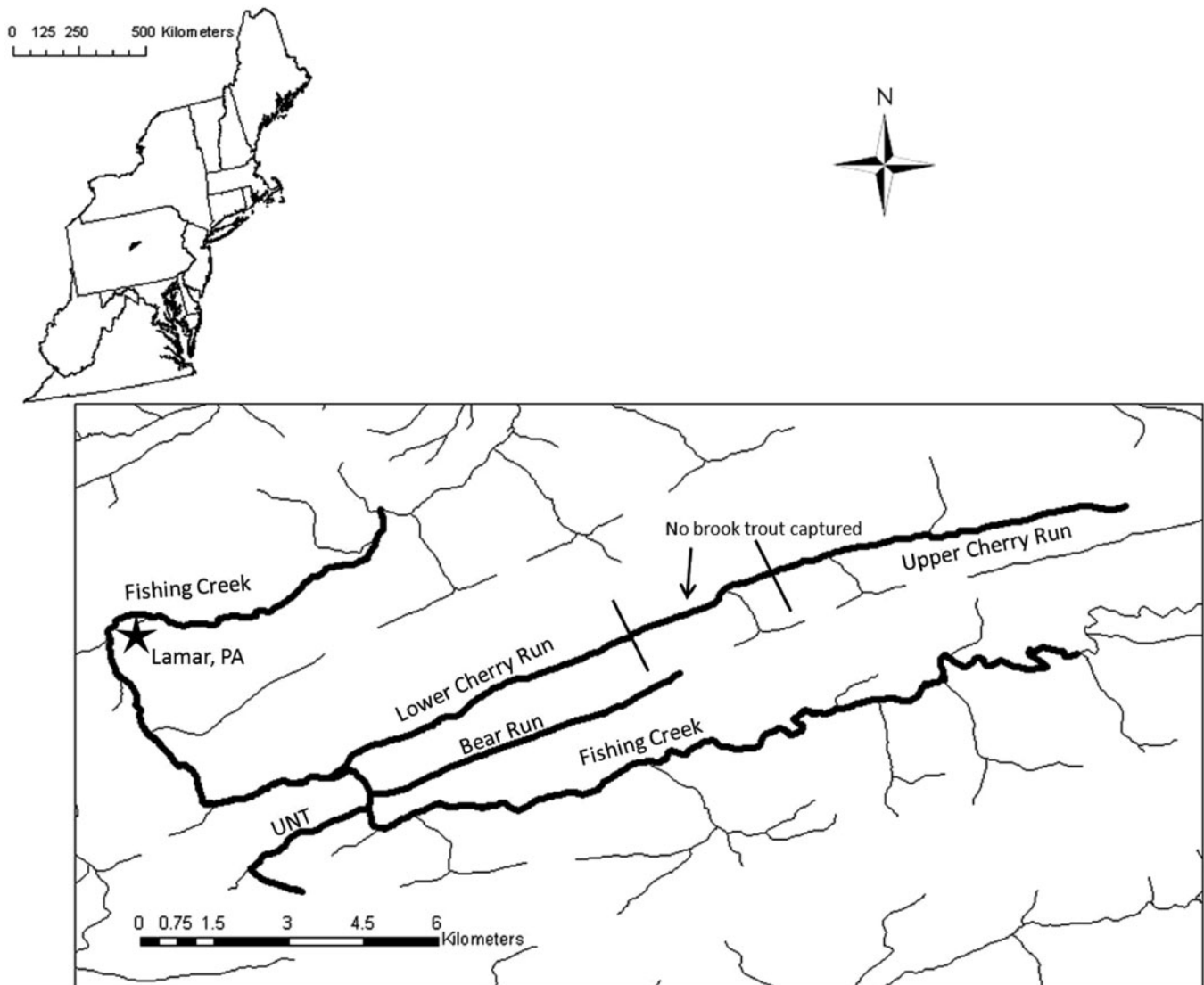


FIGURE 1. The northeastern United States (inset) showing the location of the study area in black and map of the study area in Clinton County, Pennsylvania, showing Fishing Creek and the tributaries Cherry Run, unnamed tributary 22515 (UNT), and Bear Run, shown in bold (map data source: www.pasda.psu.edu). The area between the lines in Cherry Run indicates the approximate area where no Brook Trout were sampled. Upstream from this area was considered upper Cherry Run and downstream from this area was considered lower Cherry Run.

fish movement between the upper and lower reaches. The study area was heavily forested with a mix of eastern hemlock *Tsuga canadensis* and various deciduous hardwood tree species, while agricultural land use occurred upstream of the study streams.

Quantifying stream habitat.—Because of the importance of pool habitat for salmonids (e.g., House and Boehne 1986; Sollazzi et al. 2000; Hakala and Hartman 2004), we identified and measured residual pools in the study streams using thalweg profiling. Thalweg profiling is an established method to assess pool habitat, particularly for salmonids, in small streams (Bauer and Ralph 2001; Mossop and Bradford 2006). We focused on residual pool depth as our primary measurement of habitat because (1) it is correlated with other important habitat variables (i.e.,

substrate type and water velocity), so it is ecologically relevant for fish, (2) residual pool depth can be manipulated during habitat restoration efforts and is thus a measurement that is relevant to managers, and (3) we wanted a habitat metric that could be quantified for an entire stream and would not change over the duration of our study. We developed thalweg profiles of residual pool habitat for the entire reach of Cherry Run (12.2 km) and UNT (2.4 km) using standard surveying techniques. The reach of Fishing Creek between the mouth of Cherry Run and the mouth of UNT also was surveyed (1.0 km; Figure 1). A change in elevation of ≥ 0.1 m was classified as a residual pool to eliminate minor irregularities in the streambed being considered as pool habitat (Mossop and Bradford 2006). A measurement was

recorded every 5 m and a GPS waypoint was taken either every 50 m of longitudinal stream distance or when the channel took an abrupt change of direction. Using the linear distance between the GPS points, we assigned a latitude and longitude to each measurement of the thalweg profile. Spatially referencing thalweg profile measurements created a digital map that detailed residual pools used for quantifying and classifying stream habitat and for calculating movement between fish locations.

Surgical implantation of radio transmitters.—We used backpack and towboat DC electrofishing gear to capture Brook Trout throughout the stream reaches during September and October 2010. We surgically implanted Brook Trout with Lotek Nano-Tag series digitally encoded transmitters (model NTC-3-2, 1.2 g, 124-d life expectancy; Lotek Wireless, Newmarket, Ontario). Brook Trout were anesthetized with tricaine methanesulfonate (MS-222) during the procedure. We released all Brook Trout at their capture location. Nine fish were tagged and released in lower Cherry Run, 10 in upper Cherry Run, nine in UNT, and eight in Fishing Creek. Although we did not sample for Brook Trout in Bear Run, it was monitored for use by radio-tagged fish. All of the tagged fish were age-1 or older and assumed to be sexually mature, but a confident determination of sex was generally not possible.

Radio-tracking and movement calculations.—Radio transmitters were equipped with a 12-h on-off feature and were active between 0700 and 1900 hours. Once we identified an individual Brook Trout, the location was estimated and a GPS location was recorded. Each GPS fish location was matched with the nearest thalweg profile point using the proximity tool in ArcMap (version 10.0, 2010; Environmental Systems Research Institute, Redlands, California) and the longitudinal stream distance between two consecutive fish locations was calculated. For locations that were outside of the thalweg profile in Fishing Creek, the GPS points were projected onto the Networked Streams of Pennsylvania GIS layer (Pennsylvania Spatial Data Access 1998) and the distance between consecutive locations was calculated by measuring along the stream using the measure tool in ArcMap. Movement between locations and total movement was reported as distance moved regardless of direction. Net movement was reported with respect to stream flow direction, with upstream considered positive and downstream considered negative. We classified each individual Brook Trout as lower Cherry Run, upper Cherry Run, Fishing Creek, or UNT based on where the fish had been captured and released.

Water temperature, stream flow and water quality.—HOBO ProV2 temperature loggers (Onset Computer Corporation, Bourne, Massachusetts) were deployed at locations of approximately equal distances in Fishing Creek, Cherry Run, and UNT. Water temperature was logged at 30-min intervals. We recorded the stream flow stage daily from a staff gauge that had been installed in each of the streams in order to create flow indices. Water samples were collected at base flow on 20 August 2010 and during a high flow event on 30 September 2010. Three random samples were taken near the mouth of both Cherry Run and

the UNT and in the stream reach between these tributaries in Fishing Creek. Samples were analyzed for pH and dissolved aluminum by the Pennsylvania Water Resources Research Center.

Statistical Modeling

Brook Trout movement models.—We developed competing a priori models (hypotheses) describing seasonal movement of wild Brook Trout and used generalized additive mixed models (GAMMs) to examine both linear and nonlinear relationships between Brook Trout movement and the covariates day of year (i.e., time), fish size, flow stage, and change in water temperature. For detailed descriptions of the models see the Supplement in the online version of this article. Using the gamm function in the mgcv package in R (version 2.8.1, R Development Core Team 2008), we fitted GAMMs with thin-plate regression splines using a generalized cross-validation procedure (Wood 2006). A random fish effect was included in all of the considered models to account for repeated observations on the same individual fish over time. We compared the models using Akaike information criterion (AIC) corrected for small sample size (AIC_c ; Burnham and Anderson 2002). Although there are inherent difficulties when using AIC_c to compare models with random effects (due to uncertainties in counting the number of estimated parameters), we used AIC_c because of the interest in making inferences about population-level parameters, across all fish, as opposed to inferences about particular fish in the data set (Vaida and Blanchard 2005). Prior to fitting and comparing eight competing movement models (MM), we evaluated two assumptions: temporal independence of residuals and common temporal trends in movement dynamics among study streams. To evaluate the temporal independence assumption, we first fitted a baseline model that did not explicitly model temporal correlation among residuals (MM1). Next, we fitted a spherical model to accommodate potential temporal autocorrelation (Pinheiro and Bates 2000) containing only the effect of day of the year (MM1b) and compared it with the baseline model. We investigated the spherical correlation model instead of the more commonly used autoregressive model (e.g., AR-1) because it can better accommodate missing values and irregularly spaced data (Zuur et al. 2009). We assumed temporal independence if model MM1 was the preferred model (based on AIC_c). To evaluate the assumption of common temporal trends in movement dynamics among stream reaches, we fitted a model to examine whether there were detectable differences in movement over time across the study streams by allowing a smoother to be fitted to each stream separately (MM1c). This model was investigated because we expected movement trends to differ in the stream reaches, as greater stream slope in lower order streams has been associated with less movement in stream salmonids (Chisholm et al. 1987; Kahler et al. 2001). Model MM1c was then compared with MM1 using differences in AIC_c values.

Brook Trout habitat use models in Cherry Run.—Discrete choice models with random effects were used to examine

habitat use of 20 wild Brook Trout that were located in Cherry Run (see Kneib et al. 2011 for details and the Supplement for description of models). The thalweg profile, which included the entire 12.2-km stream reach of Cherry Run, was used to create habitat categories based on the maximum depth of the residual pools. Because we did not have any a priori rationale for choosing specific residual pool depth categories, the categories were determined using a change-point analysis. The change-point analysis found thresholds in the distribution of maximum residual pool depth values. This procedure grouped the residual pools into three categories, which were described as shallow (0.10–0.26 m), intermediate (0.261–0.44 m), and deep (0.441–1.06 m). This approach yielded similar results to using the 25th and 75th quantiles of residual pool depth values, and the analysis was not sensitive to the exact cutoff between depth categories. Habitat that was not identified as a residual pool in the thalweg profile was categorized as nonpool.

Assessments of habitat use of stream salmonids may be scale dependent (Roth et al. 1996; Feist et al. 2003). Thus, we evaluated whether Brook Trout habitat selection was dependent on the spatial scale at which available habitat was quantified. Specifically, we fitted models at four different scales of available habitat based on the longitudinal stream distance from each fish location: the 250-m, 500-m, 1,000-m, and “landscape” scales. Available habitat was calculated using an equal stream distance upstream and downstream from a fish’s location to arrive at the corresponding longitudinal distance for that level (i.e., at the 250 m scale, the available habitat comprised the habitat 125 m upstream and 125 m downstream from each fish location.) The landscape model allowed the entire reach of Cherry Run to be considered available habitat for each Brook Trout location.

We fitted six competing, a priori models that represented hypotheses describing habitat selection of Brook Trout for three of the four spatial scales (250, 500, and 1,000 m; total of 18 models). Because the landscape-scale model differed in how the available habitat was quantified (i.e., available habitat did not vary over space and time), it was considered separately (total of three models). The candidate models included combinations of longitudinal pool length, day of year, fish size, and fish classified as disperser (a fish that moved 500 m or more) versus nondisperser as covariates (Supplementary Table 1). We predicted that Brook Trout would be found predominantly in residual pool habitat and that there would be selection by Brook Trout for all three residual pool categories over the nonpool category. Accordingly, the reference category for all models was set as the nonpool habitat category. This allowed us to compare selection between the three residual pool categories in each of the models compared with nonpool habitat. The discrete choice models were ranked at each of the four spatial scales using AIC. To take into account the difficulties in counting the number of parameters estimated when fitting random effects models, the equivalent degrees of freedom was used as a measure of the effective number of parameters in the models (Kneib et al. 2011).

Accordingly, AIC was calculated using the equivalent degrees of freedom as a measure of model complexity. The models were ranked based on AIC differences and Akaike weight (w_i) values. All discrete choice models were fitted using BayesX (Belitz et al. 2009).

RESULTS

Brook Trout Radio-tracking and Movement Summary

Thirty-six wild Brook Trout were captured and implanted with radio transmitters between 20 September and 2 October 2010. The mean \pm SD length and weight were 209 \pm 42 mm (range, 167–345 mm) and 98 \pm 67 g (range, 48–348 g), respectively. Individual Brook Trout were located two to three times per week during October and November 2010 and one to two times per week in December 2010. The number of days tracked and number of locations for each Brook Trout ranged from 10 to 129 d and from 3 to 42 locations, respectively. Fishing Creek Brook Trout, which were the largest fish on average (177 \pm 75 g, mean \pm SD), exhibited the most mobility and traveled the farthest distances. For example, Brook Trout from Fishing Creek were observed moving into lower Cherry Run, but they were never located in upper Cherry Run or Bear Run. In contrast, UNT Brook Trout were the least mobile and fish were never observed leaving the UNT and entering Fishing Creek. There was, however, variability in net movement among Brook Trout in all the study reaches (Figure 2), as well as total movement, which ranged from 50 to 9,000 m. For Fishing Creek Brook Trout, movement between locations ranged from 0 to 4,800 m, and their mean movement was 125 \pm 490 m. For lower Cherry Run Brook Trout, movement between locations ranged from 0 to 2,100 m, and mean movement was 150 \pm 350 m. For upper Cherry Run and UNT Brook Trout, movement between locations ranged from 0 to 775 m (mean movement, 50 \pm 115 m) and from 0 to 315 m (mean movement, 20 \pm 40 m), respectively (Supplementary Table 2).

Water Temperature, Stream Flow, and Water Quality

The ranges in water temperature in Fishing Creek, lower Cherry Run, upper Cherry Run, and UNT were 2.8–16.5°C, 0.1–17.0°C, 2.0–16.2°C, and 3.4–15.0°C, respectively. There were two high flow events during the study period; these occurred on 30 September and 1 December 2010. The patterns in stream flow stage were similar across all of the study streams. Mean \pm SD stream water pH levels during low and high flow events for Cherry Run, Fishing Creek, and UNT were 7.2 \pm 0.02 and 7.2 \pm 0.03, 7.9 \pm 0.03 and 7.6 \pm 0.04, and 6.7 \pm 0.03 and 6.7 \pm 0.06, respectively. Mean \pm SD dissolved aluminum concentrations during low and high flow events for Cherry Run, Fishing Creek, and UNT were 0.02 \pm 0.002 and 0.07 \pm 0.008 mg/L, 0.01 \pm 0.006 and 0.02 \pm 0.01 mg/L, and 0.01 \pm 0.01 and 0.03 \pm 0.003 mg/L, respectively.

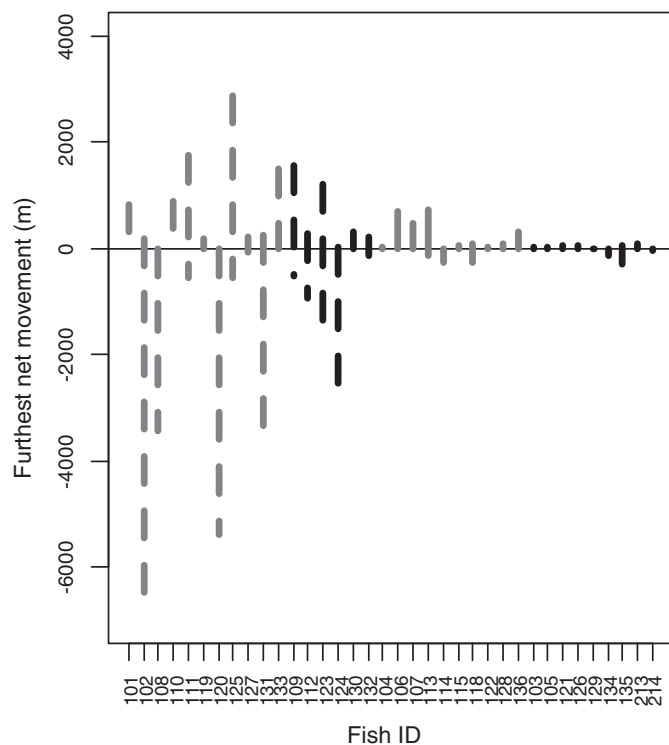


FIGURE 2. Net movement of 36 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed, Clinton County, Pennsylvania. The x -axis is the fish identifier (corresponding to the Fish ID in Table A.2) and the y -axis indicates the farthest upstream (+) and downstream (-) location for each fish relative to its release site. The dashed gray line represents Fishing Creek Brook Trout, the dashed black line represents lower Cherry Run Brook Trout, the solid gray line represents upper Cherry Run Brook Trout, and the solid black line represents UNT Brook Trout. Brook trout were classified based on where the fish was found at its last location.

Brook Trout Movement Models

We evaluated two assumptions related to fitting GAMMs: temporal independence of residuals and common temporal

trends in movement dynamics among study streams. The results of MM1b, which explicitly accounted for temporal autocorrelation ($AIC_c = 2966.12$, log-likelihood = -1475.98 , number of estimable parameters [K] = 7), compared with MM1 ($AIC_c = 2965.19$, log-likelihood = -1477.56 , $K = 5$) did not suggest that a more complex model that included an autocorrelated error structure was warranted. Therefore, we fitted all subsequent models under the assumption that the residual errors were independently normally distributed. Despite differences in stream slope, (Fishing Creek: $<1\%$ in the study area; lower Cherry Run: 1.5% ; upper Cherry Run: 2.0% ; and UNT: 5.0%) MM1c, which allowed for separate smoothers among streams ($AIC_c = 2968.37$, log-likelihood = -1472.99 , $K = 11$), provided little evidence to suggest that temporal movement trends varied among streams when compared with MM1. Therefore, subsequent movement models did not estimate separate smoothers for each stream reach.

The top-ranked movement model was MM5 ($w_i = 0.31$), which included an interaction term of day of year and fish weight (Table 1). The second-ranked model was MM6 ($w_i = 0.22$), which included an interaction term of day of year and flow. Model MM5 suggested that larger fish tended to move more in early fall than at other times, which corresponds to Brook Trout spawning season (Figure 3), and fish movement decreased into the winter regardless of fish size. Model MM6 suggested that large movements observed early in the season tended to occur during high flow events, and the amount of movement associated with higher flows declined over time (Figure 3).

Brook Trout Habitat Use Models in Cherry Run

Across the entire reach of Cherry Run, residual pool habitat percentages, calculated as the total length of each habitat category, were 14% shallow, 18% intermediate, 17% deep, and 51% nonpool. Although habitat use in Cherry Run was evaluated at the 250-m, 500-m, 1,000-m, and landscape scales, results were similar across scales. As such, we only report results for the

TABLE 1. Candidate generalized additive mixed models for describing movement of 36 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed, Clinton County, Pennsylvania (see Methods above and the Supplement for description of models: MM1–MM9). AIC_c = AIC corrected for small sample size, Δ_i = AIC_c differences, w_i = Akaike weight, K = number of estimable parameters, Log-likelihood = log-likelihood. Models are listed in descending order from the top to lowest ranked; + indicates the covariates are additive in the model, and \times indicates an interaction between two or more covariates in the model; temp = water temperature ($^{\circ}C$), weight = \log_e transformation of fish weight (g), flow = a stream flow index.

Model	Model description	K	Log-likelihood	AIC_c	Δ_i	w_i
MM5	Day of year \times weight	6	-1475.56	2963.23	0.00	0.31
MM6	Day of year \times flow	6	-1475.92	2963.97	0.73	0.22
MM3	Day of year + flow	7	-1475.21	2964.58	1.35	0.16
MM1	Day of year	5	-1477.55	2965.19	1.96	0.12
MM2	Day of year + weight	7	-1475.56	2965.27	2.04	0.11
MM7	Day of year \times temp	6	-1477.27	2966.66	3.42	0.06
MM4	Day of year + temp	7	-1477.27	2968.70	5.47	0.02
MM8	Day of year \times temp \times flow	13	-1472.60	2971.73	8.50	0.00
MM9	Day of year \times temp \times flow \times weight	18	-1468.50	2973.98	10.75	0.00

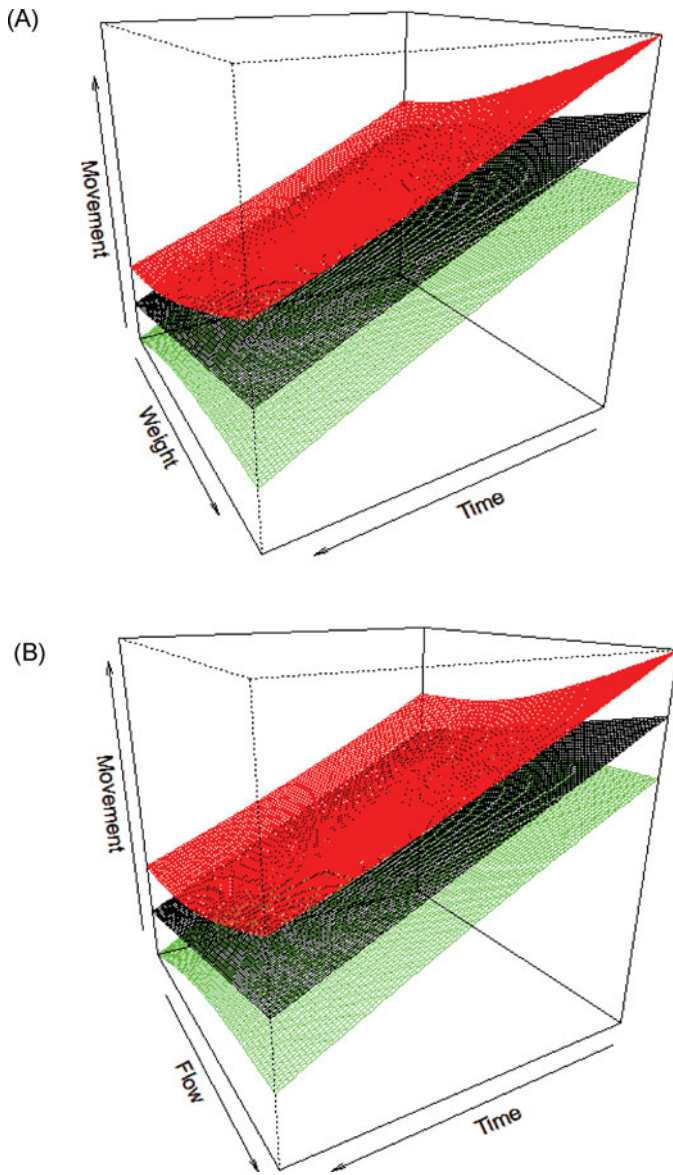


FIGURE 3. Three-dimensional plots illustrating the interaction between (A) fish size and day of year (time) and (B) flow and day of year on movement for 36 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in the Fishing Creek watershed, Clinton County, Pennsylvania. The middle surface is predicted effect from generalized additive mixed model and upper and lower surfaces are ± 2 SEs. Weight is the \log_e transformation of the weight (g) of the individual Brook Trout, flow is the change in the stream-stage flow index, day of year (time) is the grand-mean centered day of the study, and movement is the distance in meters between locations for each individual Brook Trout.

500-m scale. An unconditional model was fitted to evaluate overall selection of residual pool habitat categories compared with nonpool habitats and to quantify heterogeneity in selection among individual fish. There was an expected selection for residual pool habitat compared with nonpool habitats (Table 2), and less than 1% of fish locations occurred in nonpool habitat. However, the estimated best linear unbiased predictors (BLUPs)

TABLE 2. Parameter estimates, SD and 95% CI values, and habitat-specific variances (individual fish-specific random effects) for the unconditional discrete choice habitat use model and for the top-ranked habitat use model (model 5; Table 3) for 20 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run, Clinton County, Pennsylvania. The reference category for all models was “nonpool” habitat. $\hat{\beta}$ is the estimated preference for each of the pool habitats classified by maximum residual depth, and $\hat{\tau}_r^2$ is the habitat-specific variance describing variability in selection among individual fish.

Habitat	$\hat{\beta}$	SD	95% CI	$\hat{\tau}_r^2$
Unconditional model				
Shallow pool	4.10	0.46	3.20–5.00	0.00
Intermediate pool	3.60	0.66	2.30–4.88	3.75
Deep pool	3.85	0.61	2.65–5.05	2.73
Habitat model 5				
Shallow pool	4.67	0.96	2.80–6.54	0.00
Intermediate pool	4.42	1.02	2.41–6.43	3.67
Deep pool	3.66	1.03	1.64–5.68	2.66

indicated considerable variability among individual fish in their selection for intermediate and deep pools across all spatial scales, whereas there was little or no variability among individual fish for selection of shallow pool habitats (variances in Table 2; Figure 4). The top-ranked model ($w_i = 0.69$) included a nonparametric covariate of day of year, a nonparametric fish-specific covariate (\log_e transformed fish weight), and a nonparametric habitat-specific covariate (habitat mean length; Table 3). Since all of the covariates were modeled nonparametrically, results are provided graphically. There was an increasing selection for residual pool habitat of around 20–30 m in mean pool length and a sharp decrease in selection for habitats greater than 35 m in mean length (Figure 5). There was seasonal variation in the use of shallow and deep residual pools (Figure 6) and an increased selection of shallow residual pools occurred between October and early to mid-November, which encompassed much of the Brook Trout spawning season. During this

TABLE 3. Candidate discrete choice models with random effects describing habitat use for 20 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run, Clinton County, Pennsylvania; df is the corresponding equivalent degrees of freedom, $-2l$ is $-2 \times \log$ -likelihood, Δ_i is the AIC difference, and w_i is the Akaike weight. Models are listed in descending order from the top to lowest ranked. See the Supplement for detailed description of candidate models.

Model number	df	$-2l$	AIC	Δ_i	w_i
5	44.53	344.67	433.73	0.00	0.69
6	46.21	343.40	435.82	2.10	0.24
4	42.35	353.61	438.31	4.58	0.07
3	40.24	371.53	452.00	18.28	0.00
2	35.32	384.72	455.37	21.64	0.00
1	31.98	415.90	479.85	46.13	0.00

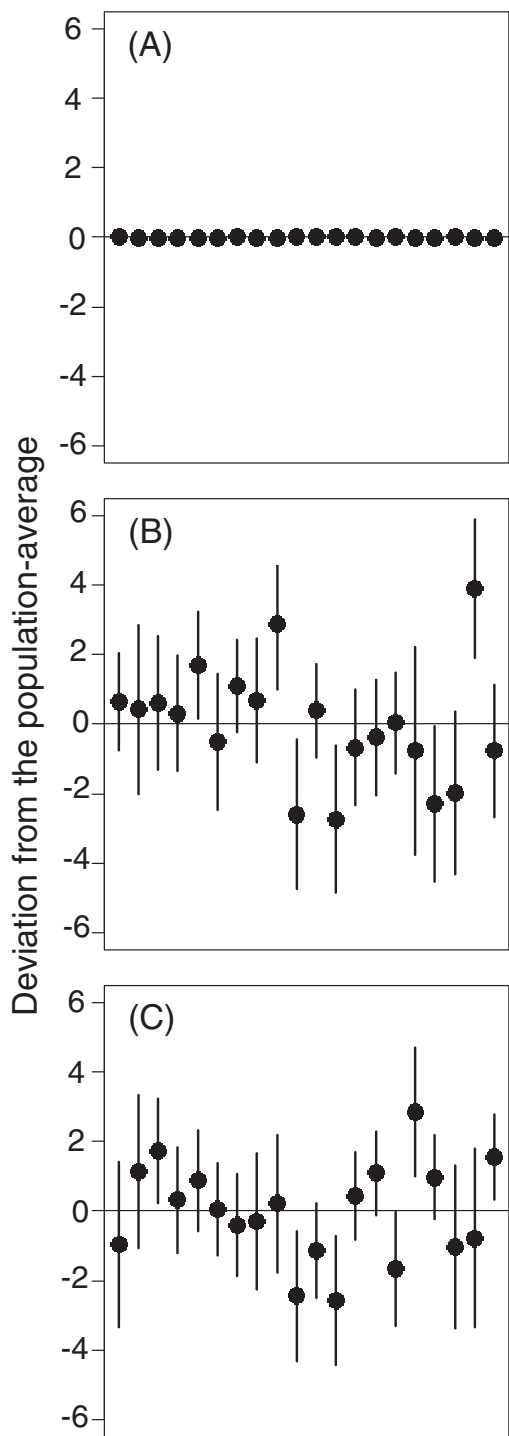


FIGURE 4. Best linear unbiased predictors (BLUPs) estimated from discrete choice models with random effects for Brook Trout illustrating individual heterogeneity in the use of (A) shallow, (B) intermediate, and (C) deep pool habitats classified based on maximum residual depth. Data are for 20 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run, Clinton County, Pennsylvania. Circles are means for individual fish and vertical bars indicate the 95% CI. A BLUP value above zero indicates that an individual fish used a habitat type more than the population average and a BLUP value below zero indicates that an individual fish used a habitat type less than the population average.

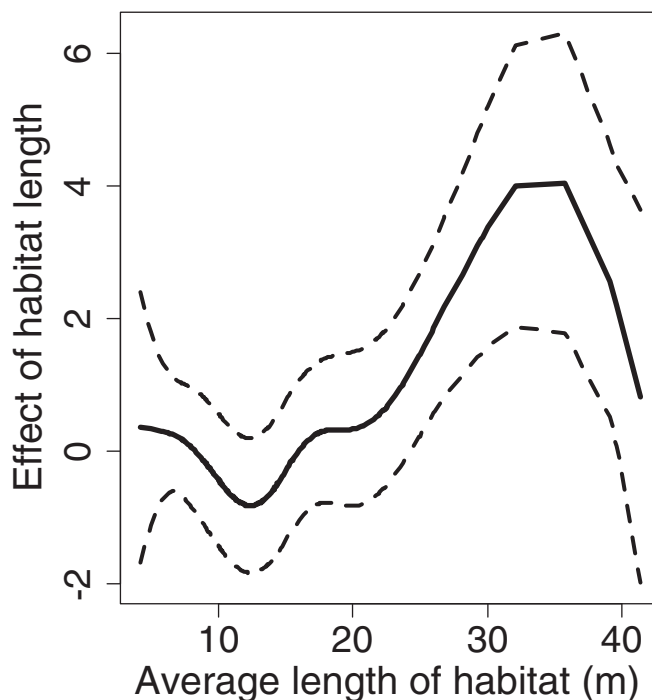


FIGURE 5. Estimated nonparametric effect of habitat length on habitat selection from discrete choice models with random effects. Analysis was for 20 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run, Clinton County, Pennsylvania. Solid line is predicted mean and dashed lines indicate the 95% CI. The x -axis is the average length of the habitat in meters in the choice sets and the y -axis shows the effect of the length of habitat on Brook Trout habitat selection.

same period, between early October (Figure 6 x -axis standardized day of the year = -1.5) and early November (x -axis standardized day of the year = 0), there was a decrease in selection of deep residual pools and then a subsequent sharp increase during the time period that corresponded with the onset of winter conditions. Fish size also was included in the top-ranked model, suggesting the use of shallow pool habitat increased as fish size increased.

DISCUSSION

We observed nonlinear movement and habitat use dynamics for wild Brook Trout, and movement dynamics were related primarily to fish size, flow, and day of year, while residual pool habitat use was a function of fish-level characteristics (fish size), habitat characteristics (pool length), and day of year. Previous Brook Trout studies have reported similar overall patterns (although often not quantifying nonlinear dynamics), showing increased movement related to spawning (Gowan and Fausch 1996), fish size (Riley et al. 1992), and flow (Gowan and Fausch 1996). However, it is important to highlight the considerable variability in movement tendencies. Across all fish, 14 Brook Trout never moved more than 200 m from their release point, while 12 fish moved >1 km and two moved >5 km. For the larger Fishing Creek Brook Trout, 4 out of 11 moved

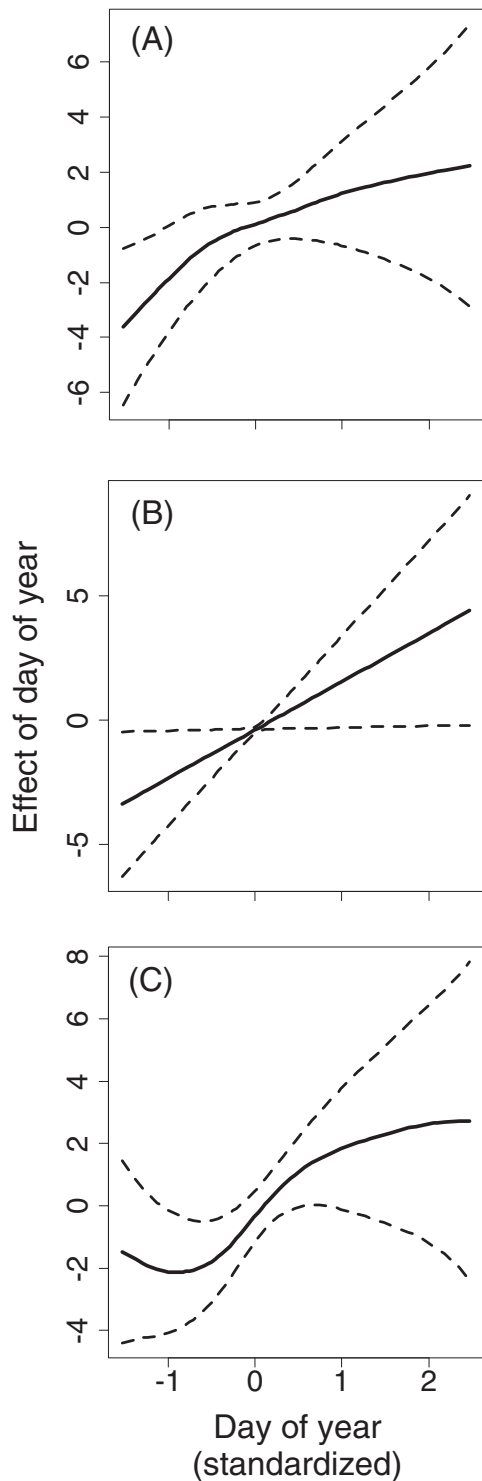


FIGURE 6. Estimated nonparametric effect of day of year on habitat selection from discrete choice models with random effects for (A) shallow, (B) intermediate, and (C) deep pool habitats classified by maximum residual depth. Analysis was for 20 wild Brook Trout radio-tracked between 20 September 2010 and 24 January 2011 in Cherry Run, Clinton County, Pennsylvania. Solid line is predicted mean and dashed lines indicate the 95% CI. The x -axis is day of year (standardized) and the y -axis shows the effect of day of year on Brook Trout habitat selection.

<1 km from their release point. This variability among fish in movement patterns has also been observed in other stream salmonids (Quinn and Kwak 2011). A notable decline in activity occurred across all Brook Trout in December when stream temperatures dropped below 7°C. We did, however, observe a single Brook Trout in lower Cherry Run move downstream ~2.5 km during December into the confluence of Cherry Run and Fishing Creek, which remained around 2°C warmer than lower Cherry Run during early winter. This movement might have been due to decreased ice formation in this area, as opposed to thermal preferences. Similar observations have been reported for Bull Trout *Salvelinus confluentus* (Jakober et al. 1998) as well as Brook Trout (Curry et al. 2002; Lindstrom and Hubert 2004). However, Chisholm et al. (1987) reported Brook Trout remained active throughout the winter in a Wyoming alpine stream system, and the movements were associated with decreased instream ice formation at higher elevations. Movement models indicated the relationship between Brook Trout size and movement was largely a function of the day of the year, and the size of a fish had less influence on movement as winter approached. Because all of the larger fish were located in the Fishing Creek, it is difficult to separate out a true “fish size effect” from a “stream effect” in this analysis. The movement models indicated a similar temporal pattern with stream flow, where the strength of the positive relationship between increasing flow stage and Brook Trout movement decreased over time. For instance, large upstream movements and increased activity were recorded during a high flow event in September, followed by little activity during a subsequent high flow event in December. Water samples taken in both Fishing Creek and the tributaries during low and high flow events did not indicate that movement was related to water quality, since pH and dissolved aluminum were below values reported to be associated with a movement response by Brook Trout in northeastern U.S. streams (pH < 5.2, dissolved aluminum > 0.15–2.0 mg/L; Baker et al. 1996).

Although movement models suggested that patterns in wild Brook Trout movement were mostly related to temporal effects, and in this particular system largely associated with spawning activity, this may not be the case for all Brook Trout populations. The spatial distribution of habitats required for spawning, overwintering, and foraging may all influence the timing and magnitude of stream-dwelling fish movements (Schoby and Keeley 2011). In addition, the high individual variability in movement tendencies and relatively small sample sizes probably reduced our ability to detect stream-specific temporal trends, if such trends were present. Habitat use also varied among individuals. Although the random effects in the habitat use models indicated there was little variability in the use of shallow residual pools by individual Brook Trout, there was relatively high variability among individual fish in the use of intermediate and deep residual pools. These results suggest that spawning behavior was a strong influence on all the Brook Trout tracked in this study, resulting in increased use of shallow residual pool habitats and little variation among fish. Whereas, habitat selection for deeper

pools was related to factors, such as thermal preferences and food availability, acting on each Brook Trout differently, resulting in a large amount of variation among fish in habitat use. In addition, interspecific and intraspecific social interactions could potentially be a factor related to individual fish habitat use. Although overall habitat selection by Brook Trout was similar for the shallow, intermediate, and deep residual pools in relation to nonpool habitats, a nonlinear seasonal trend in selection was observed. Habitat use was largely related to the day of year, and the models indicated shallow residual pools during October and November (during spawning season) were selected. Increased selection of deep residual pools was identified during December. Deeper water habitats are considered favorable to overwintering salmonids due to overhead ice cover, lack of anchor ice, and stable water temperatures (Chisholm et al. 1987; Jakober et al. 1998). The selection of particular habitats may not have been directly related to the residual depth, but to a function of other physical characteristics of shallower pools. For example, substrate size has been related to redd site selection in Brook Trout, particularly coarser substrate that is typically found in shallower stream areas (Snucins et al. 1992; Bernier-Bourgault and Magnan 2002), and in the absence of upwelling, spawning Brook Trout may select for areas of higher water velocity, possibly in shallower habitats (Essington et al. 1998; Bernier-Bourgault and Magnan 2002). Because residual depth is correlated with other important measures of fish habitat, this is advantageous for large-scale habitat use studies. For instance, residual depth measurements change slowly over time, and thus can be considered fixed during our study period and quantified across large spatial extents. This is in contrast to variables such as substrate size and velocity, which are temporally dynamic and logistically difficult to quantify for an entire stream. An additional factor that could have influenced habitat selection of Brook Trout was the presence of Brown Trout in the system. Results of several studies suggest that Brown Trout and Brook Trout fulfill similar niches (Zimmerman and Vondracek 2007), and Brown Trout often retain a competitive advantage over Brook Trout (Fausch and White 1981; DeWald and Wilzbach 1992). Therefore, Brown Trout could potentially cause Brook Trout to inhabit suboptimal habitat; however, our study design was unable to quantify these potentially important social interactions.

Overall, results from the habitat use models were similar across all four spatial scales. A failure to detect differing patterns in habitat use at varying scales suggests either that (1) in this system scale was not important because the distribution of residual pool habitat was relatively homogenous throughout Cherry Run, resulting in similar choice sets at each spatial scale, or (2) the scales chosen for this analysis were not adequate for elucidating scale-dependent relationships. For instance, if home range data were available for Brook Trout in this system, a hierarchical approach for assigning available habitat at different scales could have been used (Johnson 1980) and could have increased the ability to detect scale-dependent patterns by facilitating the identification of scale-dependent habitat covariates.

Brook Trout Conservation and Management

The observed movement patterns, habitat use, and heterogeneity among individual fish in habitat use are particularly relevant to fisheries management and stream restoration efforts. This observed heterogeneity points to the importance of maintaining (or creating) a diversity of pool habitats, as they are used differentially by individuals and seasonally. In addition, we observed a nonlinear relationship in movement and habitat use. Consideration of only linear models when assessing fish movement and habitat use could lead to incorrect inferences and potentially poorly informed management decisions. Our observations in this study underscore the value of understanding the movement dynamics of a fish species when managing for self-sustaining populations. First, it is important to maintain stream connectivity, since tributaries adjacent to the main stem of a system may provide important spawning or other critical habitat. To help maintain this connectivity, physical and environmental barriers (e.g., degraded habitat) should be minimized. Second, it is important to recognize that not all streams may be contributing equally to populations within a stream system in terms of reproductive potential, as was demonstrated by main-stem Fishing Creek Brook Trout only using lower Cherry Run for spawning, despite the availability of other tributaries. Consequently, some tributaries or areas of tributaries could be expected to be recolonized at different rates from the main stem or adjacent tributaries, or both, if local extinctions were to occur. With the threat of increased degradation of headwater stream systems, such as the continued expansion of natural gas exploration and extraction, managing entire watersheds as opposed to discrete stream reaches is particularly important for much of the remaining eastern wild Brook Trout habitat, especially considering that many populations are already isolated or fragmented.

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